genannten Zeiten dürften auch für die Tiere der Freiburger Population zutreffen. Da ich die meisten Jungtiere im Juni antraf, sollte die größte Anzahl der Begattungen etwa im April erfolgen. Stilmark (1963) fing in Sibirien trächtige Weibchen von April bis Juni, die meisten im Mai. Shubin (1964) fing in Sibirien fast nur im Mai trächtige ♀♀, stellte jedoch fest, daß einige ♀♀ im Sommer ein zweites Mal Junge werfen. Nach meinen Beobachtungen in Freiburg beginnt die Fortpflanzungszeit entsprechend der geographischen Lage gegenüber Sibirien etwa einen Monat früher. Ob in Freiburg wie in Sibirien nach Shubin Zweitwürfe vorkommen, oder ob die im Mitt- und Spätsommer auftretenden Jungtiere auch noch Erstwürfe sind, läßt sich mit Sicherheit nicht sagen.

Im Vergleich zu Japan (Hokkaido), das wahrscheinlich das Ursprungsland der hiesigen Streifenhörnchen ist, hat Freiburg ein wesentlich wärmeres Klima, aber ähnliche jährliche Niederschlagsmengen. Für die aus bedeutend kälteren Regionen stammenden Streifenhörnchen könnten zwar sehr hohe Sommertemperaturen u. U. ungünstig sein, jedoch können die Tiere sich an sehr heißen Tagen in ihren Bau zurückziehen, was sie offensichtlich auch tun. Die klimatischen Bedingungen sind für Streifenhörnchen deshalb durchaus günstig.

Das Nahrungsangebot ist für die Streifenhörnchen auf dem Friedhof wie gezeigt reichhaltig und vielseitig; eine interspezifische Konkurrenz dürfte kaum ins Gewicht fallen.

Von den bei Ognev (1966) und Freye (1968) genannten Feinden der Streifenhörnchen kommen auf dem Friedhof nur Mauswiesel, Stein- und Baummarder (?) vor; Steinkäutze, die im Untersuchungsgebiet vorkommen, und ab und zu herumstreunende Katzen können allerdings auch eine Gefahr sein.

Wesentlich für die Bestandesentwicklung auf dem Friedhof ist auch ein „Inseleffekt". Für die Hörnchen besteht kaum Veranlassung, den Friedhof, der inmitten der Stadt liegt, zu verlassen.

Schließlich kommt hinzu, daß die Tiere in ihrer neuen Umgebung wegen der anfänglich geringen Individuenzahl (Gründerindividuen) wahrscheinlich ihre Endoparasiten verloren haben[2] und dadurch von bestimmten Krankheiten oder auch nur von einer zusätzlichen Belastung ihres Energie-Budgets verschont bleiben.

All diese günstigen Faktoren lassen verstehen, daß sich hier eine Streifenhörnchen-Population gut entwickelt hat und über Jahre hält (war 1979 noch zahlreich).

Abschließend kann man sagen, daß die hiesigen Streifenhörnchen weder an Flora noch Fauna beträchtlichen Schaden verursachen. Sie fressen größtenteils Samen von Pflanzen, die für den Menschen bedeutungslos sind. Wie sich zeigte, vergreifen sie sich im Freiland kaum an Jungvögeln und wohl auch nicht an Eichhörnchen-Jungen (Mäuseversuch!).

Danksagung

Für die Unterstützung bei meiner Arbeit danke ich vielmals Herrn Prof. Dr. H. Gossow, Wien, und Herrn Prof. Dr. G. Osche, Freiburg; letzterem auch für die Durchsicht des Manuskripts. Außerdem möchte ich Herrn Prof. Dr. Niethammer, Bonn, sehr für alle Hilfe danken. Besonderen Dank gebührt auch der Friedhofsverwaltung, die mir ein nahezu uneingeschränktes Arbeiten auf dem Friedhof gestattete. Hernn Dr. R. Buchner, Freiburg, danke ich für die parasitologischen Untersuchungen. Ebenso danke ich Herrn Dr. W. Sudhaus, Freiburg, für die Durchsicht des Manuskripts. Allen namentlich nicht Aufgeführten, die mir geholfen haben, sei ebenfalls gedankt.

Zusammenfassung

Von September 1975 bis August 1976 wurde eine *Eutamias sibiricus* Population auf dem Hauptfriedhof in Freiburg untersucht. Die seit etwa 1969 bestehende Population umfaßte 1976 120 bis 150 Individuen.

Bei 16 Individuen schwankten die Aktionsräume zwischen 700 und 3975 qm. Weibchen hatten größere Aktionsräume als Männchen. Von Februar bis Juni steigerte sich die Aktivität der Tiere, fiel im Juni ab, stieg danach wieder und erreichte im September ein Maximum. Bis Mitte November sank sie auf Null. Von November bis Mitte Februar hielten die Tiere Winterschlaf.

[2] Zwei eingegangene Tiere wurden im Tierhygienischen Institut Freiburg auf Endoparasiten untersucht; der Befund war negativ.

Die Tagesaktivität zeigte im Frühling morgens, mittags und abends sehr schwach ausgebildete Pikes; im Sommer und im Herbst kamen sehr große zeitlich weitgehend übereinstimmende Schwankungen (Polyphasie) zustande, wobei im Sommer morgens und im Herbst nachmittags ein Maximum vorhanden war.

Die Fortpflanzungszeit erstreckte sich von März bis Juli.

Der größte Teil der Nahrung bestand aus Ahorn- und Lindensamen. An den untersuchten Tieren wurden keine Parasiten gefunden. Die Lebensbedingungen der Population auf dem Friedhof sind gut. Durch Streifenhörnchen verursachter Schaden an Flora und Fauna wurde bis 1976 nicht festgestellt.

Literatur

Aschoff, J. (ed), (1965): Circadian clocks. Amsterdam: North Holland Publishing comp.

Aldous, S. E. (1941): Food habits of chipmunks. J. Mammalogy **22**, 18–24.

Brand, L. R. (1974): Tree nests of California Chipmunks *(Eutamias).* Am. Midl. Nat. **91**, 489–491.

Brand, L. R. (1976): The vocal repertoire of chipmunks (Genus *Eutamias*) in California. Animal Behaviour **24**, 319–335.

Bünning, E. (1973): The physiological clock. The English Universities Press Ltd.; London: New York, Heidelberg, Berlin: Springer.

Dunford, C. (1972): Summer activity of eastern chipmunks. J. Mammalogy **53**, 176–180.

Eibl-Eibesfeldt, I. (1958): Das Verhalten der Nagetiere. In: Handb. Zoologie. Hrsg. von J. G. Helmcke. Berlin: Walter de Gruyter. Bd. **8**, 12. Lieferung, Teil 10, 1–88.

Forbes, R. B. (1966): Studies of the biology of Minnesotan chipmunks. Am. Midl. Nat. **76**, 290–308.

Freye, H.-A. (1968): Die Hörnchenverwandtschaft. Andere Murmeltiere, übrige Erd- und Baumhörnchen. In: Grzimeks Tierleben. Enzyklopädie des Tierreichs. Hrsg. von I. Eibl-Eibesfeldt, M. Eisentraut, u. a. Zürich: Kindler. Bd. Säugetiere 2, Kap. 10.

Geinitz, C. (1976): Verhalten, Ökologie und Aktivitätsperiodik des Streifenhörnchens *Eutamias sibiricus* Laxmann, 1769. Beobachtungen an einer freilebenden Population eines Friedhofsgeländes in Freiburg und an Tieren in Gefangenschaft. Dipl.-Arbeit, Freiburg.

Gossow, H. (1976): Wildökologie. München: BLV Verlagsges.

Hsu, T. C.; Benirschke, K. (eds.), (1971): An atlas of mammalian chromosomes. Vol. 5, Folio 217. Berlin, Heidelberg, New York: Springer.

Niethammer, G. (1963): Die Einbürgerung von Säugetieren und Vögeln in Europa. Hamburg, Berlin: Paul Parey.

Niethammer, J.; Krapp, F. (Hrsg.), (1978): Säugetiere Europas. Bd. 1 Rodentia. Wiesbaden: Akademische Verlagsges.

Ognev, S. (1966): Mammals of the USSR and adjacent countries. (Mammals of eastern Europe and Northern Asia). Vol. IV, Rodents. Moskau 1940. Engl. Ausgabe IPST Jerusalem, 1966.

Raths, P. (1975): Tiere im Winterschlaf. Leipzig, Jena, Berlin: Urania.

Rensch, B. (1963): Studien über klimatische Parallelität der Merkmalsausprägung bei Vögeln und Säugern. Archiv für Naturgeschichte N. F. 317–363.

Saddington, G. M. (1966): Notes on the breeding of the Sibirian chipmunk *Tamias sibiricus* in captivity. Internat. Zoo Yearb. **6**, 165–166.

Schwerdtfeger, F. (1968): Ökologie der Tiere. Demökologie. Hamburg, Berlin: Paul Parey.

Shubin, N. G. (1964): (The reproduction of chipmunk in the Tom river territory.) Zool. J. (Moskau) **43**, 910–917. (Russ., engl. Zus.)

Smith, D. A.; Smith, L. C. (1975): Oestrus copulation and related aspects of reproduction of female eastern chipmunk *Tamias striatus* (Rodentia: Sciuridae). Canad. J. Zool. **53**, 756–767.

Stickel, L. E. (1954): A comparison of certain methods of measuring ranges of small mammals. J. Mammalogy **35**, 1–15.

Stilmark, F. R. (1963): (Ecology of the chipmunk [*Eutamias sibiricus* Laxm.] in Cedar forests of Western Sayan.) Zool. J. (Moskau) **42**, 92–101. (Russ., engl. Zus.).

Stubbe, M.; Chotolchu, N. (1968): Zur Säugetierfauna der Mongolei. Mitt. Zool. Mus. Berlin **44**, 5–121.

Telegin, V. J. (1957): (Daten zur Vermehrung des Streifenhörnchens in West-Sibirien. Thesen eines Berichts der Zoologenkonferenz Sibiriens) Novosibirsk. Zit. in: Stilmark, K. F. (1963).

Vinogradov, B. S.; Argiropulo, A. J. (1968): Fauna of the USSR. Mammals, key to Rodents. Engl. Ausgabe IPST Jerusalem.

Yahner, R. H. (1978): The adaptive nature of the social system and behavior in the Eastern Chipmunk, *Tamias striatus*. Behav. Ecol. Sociobiol. **3**, 497–527.

Yerger, R. W. (1955): Life history notes on the Eastern Chipmunk *Tamias striatus lysteri* (Richardson) in Central New York. Am. Midl. Nat. **53**, 312–323.

Zimmermann, K. (1964): Zur Säugetierfaune Chinas. Mitt. Zool. Mus. Berlin **40**, 87–140.

Anschrift des Verfassers: Christian Geinitz, Institut für Biologie I (Zoologie) Albert-Ludwigs-Universität Freiburg, Albertstr. 21 a, D-7800 Freiburg

Morphology of the pectoral girdle in the Amazon dolphin Inia geoffrensis with special reference to the shoulder joint and the movements of the flippers

By M. Klima, H. A. Oelschläger and D. Wünsch

Institute of Anatomy of the Johann-Wolfgang-Goethe-University Frankfurt am Main

Receipt of Ms. 8. 2. 1980

Abstract

Studied the shoulder girdle in the Amazon dolphin *Inia geoffrensis* in comparison with that of *Tursiops truncatus* and *Phocoena phocoena*. In contrast to marine dolphins, in *Inia* the sternum takes part in the formation of the shoulder joint, the latter coming near to an enarthrosis. The well developed appropriate muscles have single, rather dispersed insertions into the humerus and render possible manifold movements of the flipper in all directions. By this *Inia geoffrensis* attains a particularly high manoeuvrability advantageous for life in the shallow waters of the Amazon river system.

Introduction

It was Dr. P. J. H. van Bree who gave us the idea of an investigation of the shoulder joint in the Amazon Dolphin *Inia geoffrensis* (Fig. 1). He drew our attention to a mounted skeleton of *Inia* exhibited in the Zoological Museum, University of Amsterdam, in the shoulder joint of which the humerus is opposed by both scapula and sternum (Fig. 2). Provided that the skeleton was mounted correctly, the formation of the shoulder joint in *Inia* had to be regarded as being unparalleled within the Mammalia on the whole.

In fact, there is known no example of a sternum that takes part in the formation of the shoulder joint in other mammals. In marsupials and placentals such as the insectivores, rodents, bats and primates, the sternum is widely separated from the scapula, both being connected indirectly with each other by means of the clavicle.

In the shoulder girdle of the Cetacea the clavicle is largely reduced. Arvy (1976) writes about the "scapular girdle" in cetaceans: "The flippers are . . . joined to the antero-lateral wall of the thorax. They are non-articulated, except where they articulate with the shoulder blades. There is never any trace of a collar bone: clearly the 'scapular girdle' does not exist." Careful investigations, however, show that the clavicle in whales has not completely disap-

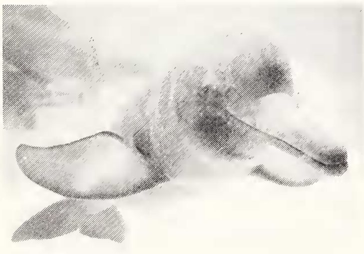

Fig. 1. Live Amazon dolphin *Inia geoffrensis* in the Zoological Garden in Dusiburg (Photo: J. Herforth). Notice the large and broad right flipper in a position of abduction and inward rotation

U. S. Copyright Clearance Center Code Statement: 0044-3468/80/4505-0288 $ 2.50/0
Z. Säugetierkunde 45 (1980) 288–309

ISSN 0044–3468/ASTM-Coden ZSAEA 7

peared. It can be traced at least in the embryos of some toothed whales (Odontoceti), e.g. *Stenella* (Klima 1978), and even in adult specimens of *Pseudorca* (Behrmann, in litt.). Within the Mammalia, retrogressions of the clavicle obviously have evolved several times in analogy to the Cetacea, since they occur in diverse terrestrial ordines showing a jumping or running mode of locomotion, e.g. the Artiodactyla, Perissodactyla (Fig. 3) and Carnivora. Within these groups, however, the sternum never takes part in the formation of the shoulder joint.

As to the anatomy of *Inia geoffrensis*, most publications have been dealing with the osteology of this species. A detailed description of the complete skeleton of *Inia* was presented by Flower (1869). Some remarks about the skeletal elements which participate in the formation of the shoulder joint, i.e. sternum, scapula and humerus, are found in the works of van Beneden and Gervais (1880), Flower (1888), Anthony (1898), Leisewitz (1921), Lönnberg (1928), Slijper (1936), van Bree and Trebbau (1974), Pilleri and Gihr (1976, 1977) and Arvy and Pilleri (1977).

The most thorough investigation of the skeleton of *Inia* on the whole (apart from Flower 1869) was carried out by de Miranda-Ribeiro (1943). In this work the author had already pointed out the possibility of an articular connection between the sternum and the humerus:

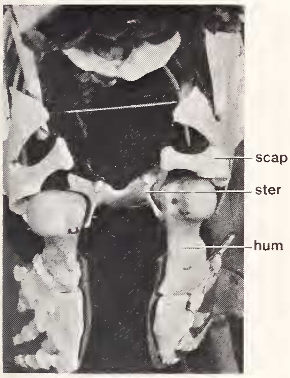

Fig. 2. The shoulder girdle in the mounted skeleton of *Inia geoffrensis* from the Department of Mammals, Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam, seen from in front. Published with kind permission of Dr. P. J. H. van Bree (For abbreviations see p. 307)

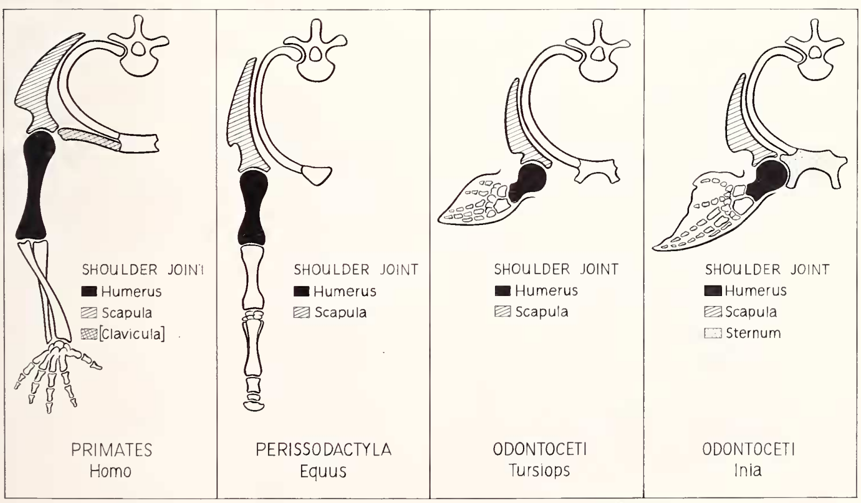

Fig. 3. Simplified diagrammatic illustration of the right shoulder joint in some placental mammals, seen from in front

"Os dois processos que Flower supôs destinados à inserçao de músculos, e que se deixam ver na face anterior, formam com o rebordo da lâmina do escudo, que lhe fica por cima, uma cavidade glénoide para a articulação da cabeça do úmero." The actual morphology of the shoulder joint in *Inia*, however, is not yet known.

The present osteo-myological investigation was undertaken in order to determine the mode of articulation and the function of the flipper in the river dolphin *Inia geoffrensis* in comparison with oceanic dolphins, especially with *Tursiops truncatus*, the Bottle-nosed dolphin. The results were considered using films of the swimming behavior of *Inia geoffrensis* and *Tursiops truncatus* in delphinaria.

Material and methods

The present investigation was carried out on the basis of the following material:

Inia geoffrensis

a. Skeleton or skeletal parts of one adult specimen each from:
- Department of mammals, Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam
- Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main
- Rijksmuseum van Natuurlijke Historie, Leiden
- Ocean Research Institute, University of Tokyo

b. Body and postcranial body, respectively, of two adult females, with the musculature preserved, from the Zoological Garden of Duisburg (kind help of Dr. W. Gewalt). Their body length amounted to 195 cm and 188 cm, respectively (cf. Gewalt 1975).

Tursiops truncatus

1 skeleton, adult specimen of 255 cm body length (loan from Mr. S. Eckardt, Frankfurt am Main)
1 juvenile specimen of 107 cm body length, with the musculature preserved (kind help of Dr. P. J. H. van Bree, Amsterdam)

Phocoena phocoena

1 juvenile specimen of 71 cm body length with the musculature preserved (kind help of Dr. P. J. H. van Bree, Amsterdam)

Lagenorhynchus albirostris

1 skeleton, adult specimen of 162 cm length from Dr. Senckenbergische Anatomie, Frankfurt am Main

Table 1

System of the toothed whales (Odontoceti) mentioned in this paper

After Norman and Fraser 1963; Rice 1977

River dolphins: Platanistidae
1. *Inia geoffrensis* Amazon Dolphin
2. *Platanista minor* Indus Dolphin
3. *Pontoporia blainvillei* La Plata Dolphin
Ocean dolphins: Delphinidae
1. *Delphinus delphis* Common Dolphin
2. *Lagenorhynchus albirostris* White-beaked Dolphin
3. *Tursiops truncatus* Bottle-nosed Dolphin
Phocoenidae
1. *Phocoena phocoena* Harbor Porpoise

The bodies of *Inia geoffrensis, Tursiops truncatus* and *Phocoena phocoena* were dissected and investigated with the methods of macroscopical anatomy. Moreover, tissue samples were taken from the sternal part of the shoulder joint cavity in *Inia geoffrensis* and processed histologically into stained and coverslided sections. In order to analyze the movements of the flippers, films in normal and in high speed (24 and 64 frames/s) were taken of *Inia geoffrensis* and *Tursiops truncatus* at the Duisburg Zoo.

Morphology and function of the pectoral girdle

Sternum

The morphology of the sternum in *Inia geoffrensis* is quite atypical for a member of the toothed whales (Odontoceti). It is a broad, flat and unsegmented bony element (Fig. 4). There is no division into manubrium and sternebrae like in other Odontoceti and most mammals. The sternum is nearly hexagonal in shape and shows a marked cranial projection which is deeply clefted into two digitiform processes, the cranial processes of sternum. In its cranial half the sternum shows rather flat, paired lateral and ventral projections with sharp distal edges, the lateral and ventral processes of sternum. The three projections on each side of the sternum which are orientated perpendicular to each other, together form a broad and shallow accessory groove for the proximal end of the humerus (lesser tubercle, see below). Four pairs of ribs attach to the sternum.

In contrast to the conditions in *Inia*, the sternum in *Tursiops* (Fig. 4) is typical for a member of the Odontoceti. It is divided into the broad manubrium and two or more slender sternebrae. Separate sternebrae regularly occur in young animals and co-ossify later, but residues of the sutures remain between the sternocostal articulations of both sides. Usually there are five or six pairs of true or vertebrosternal ribs in *Tursiops.* There are no sternal projections with the exception of flat lateral processes on the lateral borders of the manubrium. In *Tursiops*, however, these processes do not take part in the articulation of the humerus.

Because of its shape and its three different processes forming an accessory osseous joint cavity for the humerus on either side, the sternum of *Inia* seems to be unique within the Cetacea and even the Mammalia on the whole. No comparable structure occurs in other toothed whales (Odontoceti). Like in other Odontoceti, however, the sternum in *Inia* has a great relative size, approximately amounting to 8% of the total length of the skeleton. Thus, the sternum forms a stable anteromedial portion of the ventral wall of the thorax and pro-

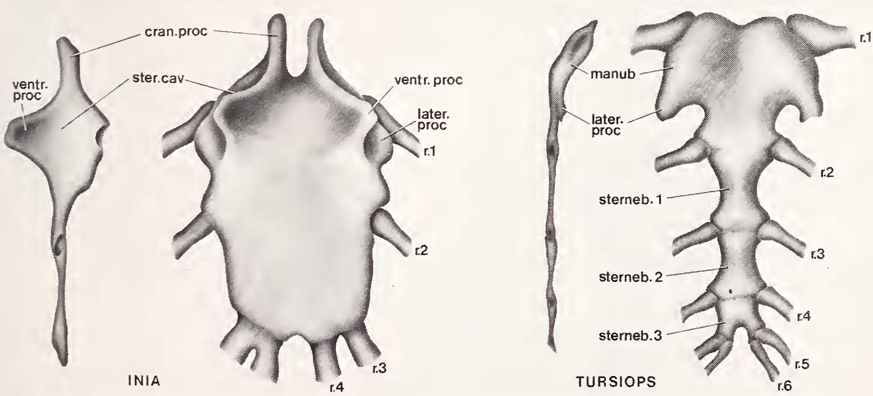

Fig. 4. Sterna of *Inia geoffrensis* and *Tursiops truncatus* in lateral aspect (on the left) and ventral aspect (on the right). Notice the broad accessory joint cavity in *Inia* situated between the specific lateral, ventral and cranial processes of the sternum (For abbrev. see p. 307).

vides a broad area of origin for the infrahyal, cervical, pectoral and abdominal muscles. In whalebone whales (Mysticeti), the single-pieced sternum is a rudimentary element of very small size; its length amounts to 1.4–3.5% of the total length of skeleton (KLIMA 1978). Here the sternum is linked with the first pair of ribs only, thus forming a very incomplete ventral connection between both halves of the thorax. Because of its small relative size, the sternum in whalebone whales is of minor importance for the attachment of the infrahyal and the pectoral musculature.

Scapula

In *Inia* (Fig. 5 a) the scapula shows the same basic shape as in most members of the Odontoceti (Fig. 5 b). It is a large, flat triangular bone. Like in all Odontoceti, its vertebral border (margo medialis) is rounded, its posterior border (margo inferior) is slightly concave. The broad and flat acromion does not form the summit of the shoulder in order to roof the glenoid cavity, but points cranialward as a projection of the front border of scapula (margo superior), next to the anterior rim of the glenoid cavity.

In spite of basic agreements, the scapula of *Inia* differs in several features from that of the marine dolphins as for instance *Tursiops,* and obviously shows a more primitive condition (Fig. 5). *Inia* has a low spina scapulae extending into the acromion and separating the suprainatous and infraspinatous fossae. Like in *Pontoporia* (STRICKLER 1978), the supraspinatous fossa is rather broad and deep and serves for the origin of the powerful Supras-

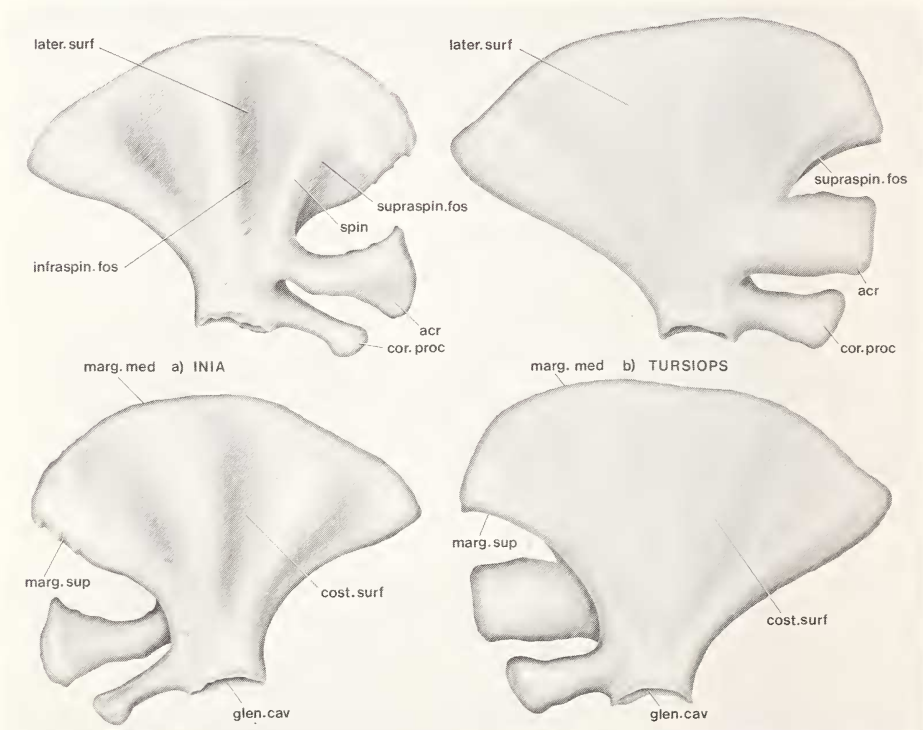

Fig. 5. Right scapulae of *Inia geoffrensis (left)* and *Tursiops truncatus (right)*. Lateral surface of scapulae above, costal surface of scapulae below. Notice the long coracoid process which points ventralward, and the broad concavity of the supraspinatous fossa in the scapula of *Inia* (For abbrev. see p. 307).

pinatus. The infraspinatous fossa is broad and shallow but still distinct, like the groove of the Teres major which originates in the posterior part of the lateral surface of scapula.

In *Tursiops,* however, no trace is left of the spina scapulae. The acromion and the lateral surface of scapula lie exactly in the same plane. The supraspinatous fossa is only vestigial and appears as a narrow notch at the anterior end of the margo superior.

Further differences between the scapulae of *Inia* and *Tursiops* consist in the orientation of the acromion and the coracoid process to each other (Fig. 5). In *Inia* both projections lie in different planes, forming a wide gap for the passage of the strong Supraspinatus (dorsoventral aspect). In *Tursiops* this gap is rather narrow. Moreover, the coracoid process in both species points into different directions. In *Tursiops* it projects cranialward, forming only a very small angle with the acromion (lateral aspect). In *Inia,* the coracoid process points slightly cranioventralward, inclining toward the sternum and thus forming a wider angle with the acromion. This inclination of the coracoid process in *Inia* obviously has a certain significance for the connection of scapula and sternum, established by the Pectoralis minor.

As to the shape of the scapula, *Inia* shares more common features with the terrestrial mammals than *Tursiops* does. The more complex surface morphology of the scapula in *Inia* stands for a high differentation of the corresponding muscles capable of complicated and extensive movements of the flipper (cf. PILLERI et al. 1976 for *Platanista;* STRICKLER 1978 for *Pontoporia*). Similar conditions are to be expected for the movements of the scapula in *Platanista* and *Pontoporia*, whereas in *Inia* the mobility of the scapula is somewhat restricted because of its unusual connection with the shoulder joint. In *Tursiops* and other marine Odontoceti the scapula shows a relatively simple surface morphology. Here the scapula obviously gives rise to less differentiated muscles responsible for comparatively uniform movements of the flipper.

Humerus

The humerus in *Inia* (Fig. 6) is short and stout. It consists of a large, rounded proximal head, a broad, flattened body or shaft in the middle, and a distal condyle which is slightly convex. The distal condyle articulates with the radius and the ulna. The head of humerus, which is nearly hemispherical, merges at its circumference in an irregularly shaped neck. On the medioventral side of the latter a broad rugged process rises, which is nearly oval in shape, the lesser tubercle of humerus. As it lies almost in one curvature with the surface of the head of humerus, the lesser tubercle can be regarded as some kind of an accessory condyle of the humerus which articulates with the sternum. The exceptionally broad lesser tubercle, into which the strong Subscapularis is inserted, fuses to the relatively small greater tubercle. The latter is situated directly at the proximal end of the radial border of the humerus shaft, thus serving for the insertion of the well developed Supraspinatus. The greater tubercle and the head of humerus are separated by a deep notch representing the cavity for the subdeltoid bursa, the configuration of the three projections otherwise being comparable with that in *Homo* (Fig. 6).

The outer (radial) border of the humeral shaft in *Inia* runs from the greater tubercle to the rather prominent lateral epicondyle and as a sharp bony rim supports the proximal part of the outer (radial) edge of the flipper because in Odontoceti (compared with terrestrial mammals) the anterior extremity normally is held in a position of inward rotation, the radial edge of the humerus shaft (margo lateralis) together with the greater tubercle points cranioventrally, whereas the lesser tubercle points medioventrally. On the opposite side the sharp inner (ulnar) border of the humeral shaft runs from the head of humerus to the slightly prominent medial epicondyle and supports the proximal part of the inner (ulnar) edge of the flipper. Between both edges of the humeral shaft there are two broad planes, the dorsolateral and the medioventral surfaces of humerus. The proximal part of the dorsolateral surface, near to the neck of humerus, bears a rough elevation, the deltoid tuberosity, for the insertion of the Deltoideus (not labeled in Fig. 6). The medioventral surface near to its ulnar border serves as a broad insertion area for the Pectoralis major and the Latissimus dorsi. In *Pontoporia blainvillei,* the La Plata Dolphin, the osteology of humerus and scapula is nearly identical with that of *Inia* (cf. STRICKLER 1978).

The humerus in *Tursiops,* however, like in other marine Odontoceti (e.g. *Lagenorhynchus albirostris*) differs from that in *Inia* in several important features. Being approximately of the same thickness, it is much shorter and its borders are not edged but rounded. The most important differences concern the position of the greater and lesser tubercles. In *Inia* both tubercles adjoin each other and are partially fused, whereas in *Tursiops* they have completely merged in one massive and strongly prominent common tubercle. The different positions of the tubercles are most conspicous in the cranial aspects of both humeri (Fig. 6; diagrams at right showing the angles between the greater tubercle and the common tubercle, respectively, and the radial border of humerus). Whereas in *Inia* and *Pontoporia* the head of humerus and both tubercles principally show the same arrangement as in *Homo,* except that in *Inia* the tubercles have a reciprocal size and are not separated by the cavity of the deltoid bursa, a clearly different situation is found in *Tursiops.* Like in *Lagenorhynchus,* the whole proximal end of the humerus seems to have been "rotated" by approx. 90° outward about the axis of the flipper so that the resulting common tubercle projects from the dorsolateral surface of humerus. The shoulder girdle of *Phocoena phocoena,* another marine dolphin, however, obviously differs from those of *Tursiops* and *Lagenorhynchus* in the position of both the head of humerus and the (single) tubercle (cf. SMITH et al. 1976). – Whether it is correct to derive the morphology of the proximal end of the humerus (head of humerus, tubercles) in *Tursiops, Lagenorhynchus* and *Phocoena* from the conditions in *Inia* and *Pontoporia* and whether the tubercles in whales are homologous to those in primates (*Homo*) has to be shown by further detailed investigations.

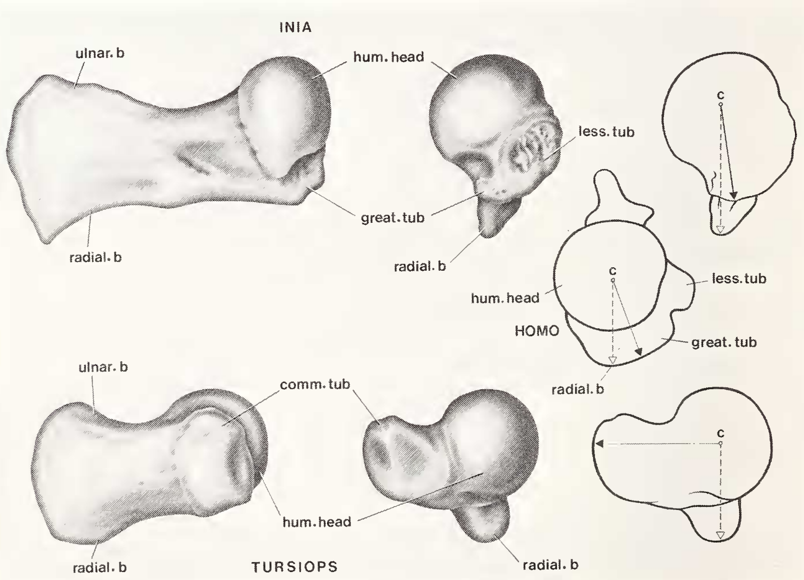

Fig. 6. Right humeri of *Inia geoffrensis (above)* and *Tursiops truncatus (below).* Dorsolateral aspect on the left, cranial aspect in the middle. Diagrams on the right show the angle between the greater tubercle (black arrow) and the radial border (white arrow) of humerus in *Inia (above)* and in *Homo (center)*, and between the common tubercle (black arrow) and the radial border of humerus (white arrow) in *Tursiops*, respectively *(below)*. In *Homo* the radial border is not to be seen (level marked by radial b). (For abbrev. see p. 307), Combined after FICK (1904), GRAY (1973) and FRICK–LEONHARDT–STARCK (1977)

From the standpoint of functional morphology, the differences between the humeri in *Inia* and *Tursiops* as to their shape and to the location of their tubercles can be interpreted as follows. In *Inia* and *Pontoporia,* which obviously represent the more primitive (plesiomorphous) conditions, the proximal part of the humerus on both its dorsolateral and medioventral surfaces shows a series of distributed insertion areas and low projections, respectively, into which single muscles are inserted, the greater tubercle being the smaller one. The whole set of strongly differentiated muscles should render possible manifold and extensive, but perhaps less powerful movements of the humerus. In *Tursiops* and *Lagenorhynchus,* however, which obviously represent a derived (apomorphous) condition, the highly prominent common tubercle, which arises from the dorsolateral surface of humerus, is concentrating the tractive power of several muscles to one point or its distal edge, respectively (high moment of rotation). In *Tursiops* and *Lagenorhynchus* these muscles therefore should render possible more powerful movements of the flipper in only a few directions, especially the movements upward (extension) and forward (abduction).

Structure of the shoulder joint

The shoulder joint in *Inia* comprises three bony elements, scapula, humerus and sternum (Figs. 7–8, 11–12, 14). In it the globular head of humerus is opposed by the cup-like "acetabulum" formed by the glenoid cavity of the scapula and the accessory joint cavity of the sternum (c.f. Klima et al. 1979). In contrast to the conditions in *Tursiops* and in most mammals (including man) where the shoulder joint represents a simple spheroidea (Articulatio spheroidea; Nomina anatomica, Tokyo), in *Inia* more than half of the humeral head is held in the "acetabular" cavity, the joint coming close to the hip point in terrestrial mammals (Enarthrosis globoidea, Fick 1904; Enarthrosis, Braus 1921; Terry 1947). Only the head of humerus and the glenoid cavity of the scapula as the primary parts of the shoulder joint are covered with a layer of hyaline cartilage. The secondary (accessory) joint cavity of the sternum, however, is coated by a thick layer of collagen and elastic fibers (Fig. 10). These fibers are part of the broad aponeurosis of the Pectoralis minor.

The synovial cavity, which is filled with the synovial fluid, is enclosed between the surfaces of the humeral head and the glenoid cavity of scapula; it extends into the widespread and folded articular capsule (Fig. 14D). The synovial cavity dorsomedialward slips under the Subscapularis; medioventralward, in some phases of movement, it slips under the lateral

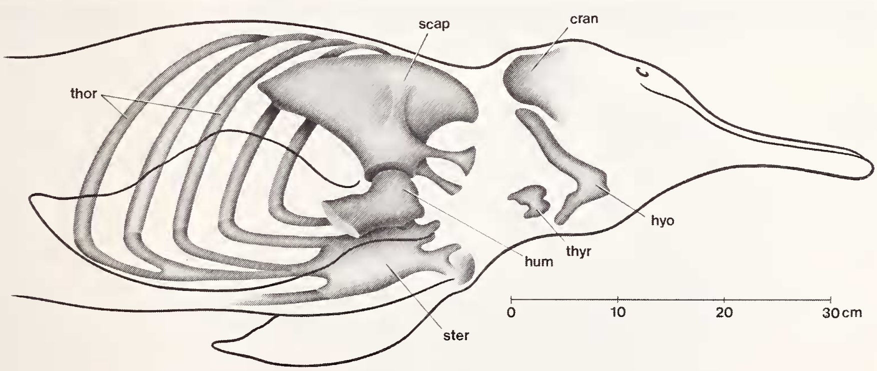

Fig. 7. Ventrolateral aspect of the right side of *Inia geoffrensis*, showing the position of the shoulder girdle. For better orientation, the same ventrolateral aspect is used in the Figures 8, 11–12, 13, 14 A–C (For abbrev. see p. 307)

border of the accessory joint cavity of the sternum. A large synovial bursa, the subscapular bursa, lies within the folded capsule beneath the tendon of the Subscapularis and communicates with the synovial cavity. Another synovial bursa, the subdeltoid bursa (Fig. 14B), is situated between the medial surfaces of the Deltoideus and the Supraspinatus on the one hand and the articular capsule on the other hand. It does not communicate with the synovial cavity.

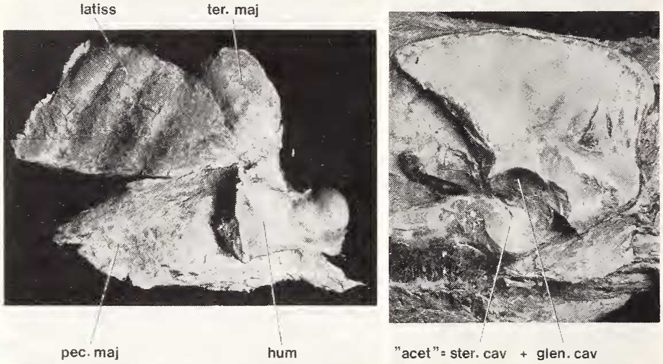

Fig. 8. Inia geoffrensis. Photographs showing the removed humerus *(left)* and the corresponding complex joint cavity of scapula and sternum *(right)*. Same ventrolateral aspect as in Fig. 7

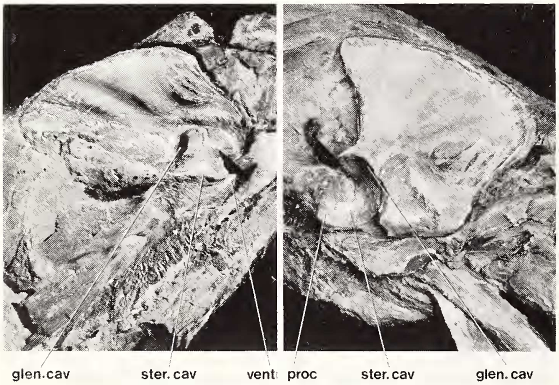

Fig. 9. Inia geoffrensis. Photographs of the complex cavity of the shoulder joint in different aspects to show its quality as an enarthrosis. *Left:* ventrolateral aspect, slightly from caudal. *Right*: same aspect, slightly from cranial

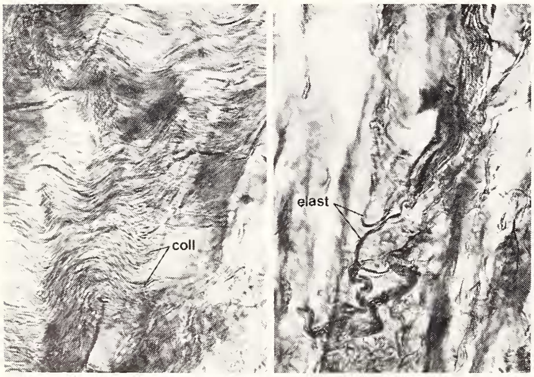

Fig. 10. Inia geoffrensis. Connective tissue taken from the surface of the accessory joint cavity for the humerus, formed by the sternum. The tissue consists mainly of bundles of parallel collagen fibers (coll) and of single curled elastic fibers (elast) (Sections stained with resorcin-fuchsin, magnification 400 X)

The articular capsule of the shoulder joint is strengthened by several ligaments. The glenoid ligament (Fig. 14C) encircles the posterior part of the glenoid border of the scapula, giving some fibers to the sternoglenoidal ligament and to the very strong glenohumeral ligament. The narrow sternohumeral ligament (Fig. 14A) extends between the ventral process of sternum and the dorsolateral surface of humerus.

Outside the articular capsule, the thin sternoacromial ligament (Fig. 14B–D), which runs parallel to the Pectoralis minor, again stabilizes the connection between sternum and scapula. In the cranial part of the scapula there are three ligaments supporting the Subscapularis, the Supraspinatus and the Deltoideus (Fig. 14B). They are the acromiomarginal, coracomarginal and coracoacromial ligaments.

Movements in the shoulder joint

Theoretically, the shoulder joint in *Inia* as a specialized spheroidea (enarthrosis; Terry 1947) is capable of movements around an indefinite number of axes. The following three of them are considered the main axes, permitting three main kinds of movement: 1. the longitudinal axis of the shoulder joint (parallel to body axis) for extension and flexion, 2. the sagittal (dorsoventral) axis of the shoulder joint for abduction and adduction, and 3. the longitudinal axis of the humerus for outward and inward rotations. The actual movements of the flipper more or less are a combination of these main kinds of movement, being characterized as follows (Fig. 11; for orientation see Fig. 7).

Extension: The humerus is moved dorsalward, i.e. the flipper is raised.
Flexion: The humerus is moved ventralward, i.e. the flipper is depressed.
Abduction: The humerus is moved lateralward, i.e. the flipper is drawn forward.
Adduction: The humerus is moved medialward, i.e. the flipper is drawn backward.

Outward rotation: The humerus is turned outward around its longitudinal axis, i.e. the front border (radial edge) of the flipper is rotated upward.

Inward rotation: The humerus is turned inward around its longitudinal axis, i.e. the front border (radial edge) of the flipper is rotated downward.

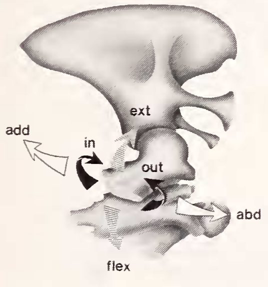

Fig. 11. Diagram showing the main possibilities of movements in the shoulder joint of *Inia geoffrensis*: extension (ext) and flexion (flex), abduction (abd) and adduction (add), inward rotation (in) and outward rotation (out). Same ventrolateral aspect as in Fig. 7

Muscles of the neck and shoulder

After removal of the well developed, rather thick panniculus carnosus of *Inia* in the neck and shoulder girdle region, the corresponding superficial muscles appear (Figs. 12, 13). In lateral view of the neck, the greatest muscle is the Sterno-humero-mastoideus complex. In *Inia* like in *Platanista* (Pilleri et al. 1976) this muscle complex is particularly large and strong compared with that of *Tursiops* and other Odontoceti (*Delphinus,* l.c.). In *Inia* the Sterno-humero-mastoideus complex is divided into two parts, both of them being inserted into the lateral surface of the mastoid process by a strong (common) tendon. The medioventral part of the complex consists of one long sternal head arising from the medial side of the ventral process of sternum, the Sternomastoideus. The dorsolateral part has two heads, both arising from the humerus, the first one from its radial border, the second one further dorsally from the dorsolateral surface of humerus. These two heads together represent the Mastohumeralis. The dorsal head of the latter is fused to the Omohyoideus which crosses beneath the remaining part of the Sterno-humero-mastoideus complex.

The division of the Mastohumeralis into two heads together with the fusion of its dorsal head with the Omohyoideus is the most conspicous feature of the whole Sterno-humero-mastoideus complex. We have found these conditions in both specimens of *Inia* examined. Although a certain variation within the species cannot be excluded, it seems very probable

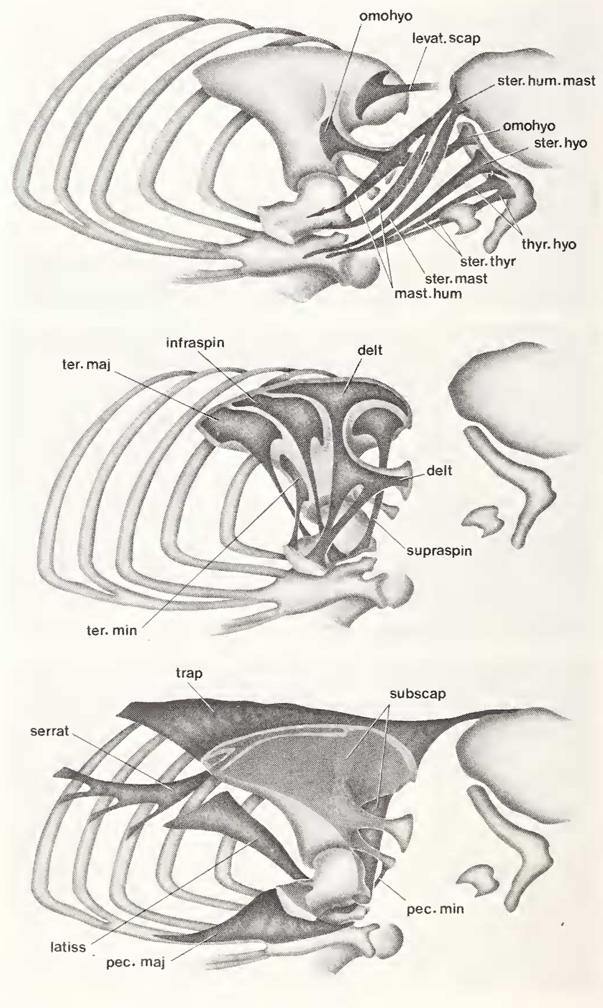

Fig. 12. Diagram showing the arrangement of some muscle groups of the neck and shoulder girdle region in *Inia geoffrensis.* Same ventrolateral aspect as in Fig. 7 (For abbrev. see p. 307).

that this arrangement of muscles has to be regarded as a characteristic of *Inia* only. On the one hand, the functional significance of this muscle complex may lie in the reciprocal fixation and movement of the head and humerus. The powerful muscles situated on both sides can flex the neck ventralward and can bring the head either sideward or downward, according to their unilateral or bilateral action. This peculiar mobility of the head in *Inia* is well known (cf. PILLERI et al. 1976 for *Platanista*). If the head is fixed, however, the muscle complex can abduct the humerus. On the other hand, the Sterno-humero-mastoideus together with the Omohyoideus may be important for the fine adjustment of scapula, humerus, sternum and cranium to one another and for the stabilisation of the shoulder joint.

Apart from the Sterno-humero-mastoideus complex, the strong infrahyoid musculature also contributes to the considerable mobility of the head in *Inia* on the one hand, and to the fixation of the sternum (and the shoulder girdle) on the other hand. The latter group consists of the Sternohyoideus, Sternothyroideus and Thyrohyoideus, together with the Omohyoideus. Like the Sternohumero-mastoideus complex the infrahyoid musculature shows a certain tendency to split up and form new heads. Parts of both the Sternothyroideus and Thyrohyoideus are separate and have fused into one portion which runs lateral from the thyroid cartilage and is inserted into the hyoid bone.

The Trapezius of *Inia* is well developed. It is inserted almost into the whole vertebral border (margo medialis) of the scapula (cf. PILLERI et al. 1976 for *Platanista*). In its anterior, most cranial part, muscle fibers appear which obviously belong to the Rhomboidei but cannot be separated.

The Levator scapulae originates from the outer surface of the deltoid fascia, at the level of the supraspinatous fossa, and is inserted into the cervical vertebrae. The Omohyoideus arises from the deltoid fascia, too, at the level of the basis of the acromion, to be inserted into the hyoid bone.

Muscles of the shoulder and arm

After removal of the superficial muscles and of the common deltoid and infraspinatus fasciae, the deep muscles appear (Fig. 12, 13). The Deltoideus covers more than half of the lateral surface of the scapula and the major part of the lateral surface of the shoulder joint. It arises from the anterior half of the vertebral border (margo medialis) and from the adjacent part of the lateral surface of scapula, as well as from the spine and the acromion. Its posterior margin overlaps the Infraspinatus. The Deltoideus inserts into a broad tuberosity on the dorsolateral surface of humerus (no lettering in Fig. 6); on the whole it extends the flipper and rotates it outward. Its acromial part abducts the flipper forward, and, if rotated outward, rotates in inward (exact course of muscle see in Fig. 13).

After removal of the Deltoideus, the Supraspinatus appears (Fig. 14A). It arises from the supraspinatous fossa, the inner (medial) side of the acromion and the acromiomarginal ligaments (Fig. 14B), to be inserted into the (small) greater tubercle. The powerful muscle abducts the flipper and rotates it outward, if rotated inward, and rotates it inward, if rotated outward.

Medial and caudal to the Deltoideus arises the broad Infraspinatus, being inserted distal to the Supraspinatus, near the radial border of humerus. The Infraspinatus adducts the flipper and rotates it outward. Caudal to the Infraspinatus, on the lateral surface of scapula near its posterior border, there arise dorsally the strong Teres major and ventrally the small Teres minor. Both attach to the humerus near its ulnar border, the Teres major on the dorsolateral, the Teres minor on the medioventral surface. They adduct the flipper and rotate it inward, if rotated outward.

Nearly the whole medial (costal) surface of scapula gives origin to the powerful Subscapularis (Figs. 12, 14C, D). The area of origin includes the broad and firm interosseous membrane stretching between the margo superior and the coracoid process (Fig. 14B) and

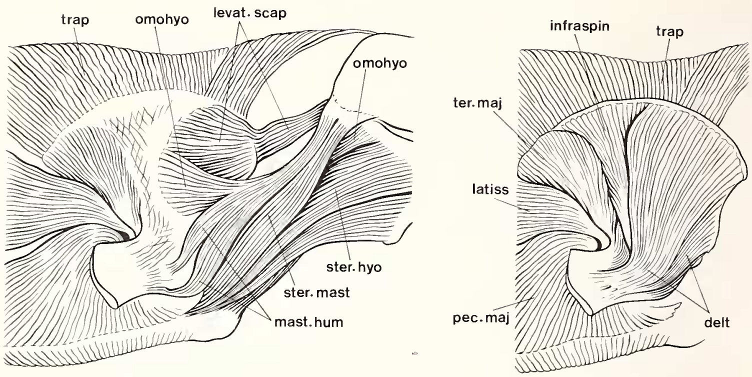

Fig. 13. Morphology of the musculature of the neck and shoulder girdle in *Inia geoffrensis.* Same ventrolateral aspect as in Fig. 7. *Left:* superficial layer. *Right:* deep layer. (For abbrev. see p. 307)

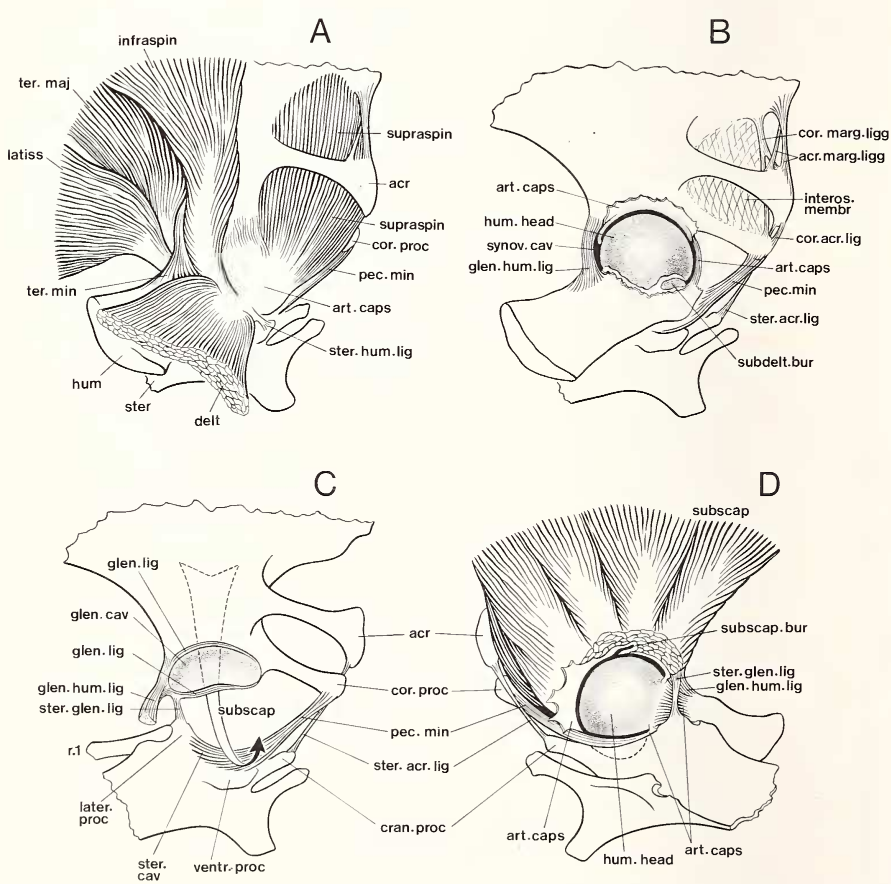

Fig. 14. Morphology of the muscles, ligaments and articular facets of the shoulder joint in *Inia geoffrensis.* Figs. A–C same ventrolateral aspect as in Fig. 13, after removal of superficial layers. Fig. D in dorsomedial aspect. (For abbrev. see p. 307)

supporting the Supraspinatus which runs at its lateral side. The Subscapularis is inserted with a broad tendon into the large (oval) lesser tubercle. It flexes and rotates the flipper inward and assists in both abduction and adduction by the contraction of its anterior and posterior parts, respectively.

The Pectoralis minor runs parallel to the Subscapularis and Supraspinatus muscles, being embedded between their front borders. It arises with a flattened fibrous aponeurosis from the broad area between the lateral, ventral and cranial processes of the sternum (accessory osseous joint cavity for head of humerus) and is inserted with a thin muscular part into the tip of the coracoid process. As to the circumduction of the scapula, which is limited anyway, the contraction of this small muscle is of only minor importance. The main function of the Pectoralis minor is to fix the scapula at the sternum. i.e. to stabilize the complex joint cavity for the humerus. Moreover, it serves as a coating of the accessory osseous joint cavity formed by the sternum (see p. 6).

From the chest and trunk there arise two strong muscles, both being inserted into the ventromedial surface of the humerus, near its ulnar border. The first one, the Pectoralis major, on the whole flexes the flipper and rotates it outward. Its posterior portion assists in the adduction, the anterior portion in the abduction of the flipper. The second one, the Latissismus dorsi, mainly serves as a strong adductor, assisting in the inward rotation of the flipper, if rotated outward.

The Serratus anterior, which arises from the thorax, is inserted into the vertebral border (margo medialis) of the scapula and rotates it caudalward and ventralward.

Muscle action

In general, the musculature of the shoulder girdle region has two main functions, the separate movement 1. of the scapula and 2. of the humerus, both of which normally are combined in the actual movements of the flipper. In *Inia,* however, the mobility of the scapula is rather restricted because of its indirect linkage with the sternum, which takes part in the formation of the shoulder joint. Therefore the most extensive movement of the scapula should be its rotation around the shoulder joint, the sternum being some kind of fixed point.

In detail, movements of scapula and humerus are caused mainly by the action of the following muscles (see Fig. 11 and 12):

Dorsalward elevation of the scapula (limited): directly by the Trapezius on the whole and the Rhomboidei, indirectly by the Latissimus dorsi.

Ventralward depression of the scapula (limited): directly by the most cranial head of the Serratus anterior and (only slightly) the Pectoralis minor; indirectly but powerful by the Pectoralis major and the Subscapularis.

Cranialward displacement of the scapula (limited): by the anterior part of the Trapezius and of the Rhomboidei, by the Levator scapulae and the Omohyoideus, and indirectly by the Mastohumeralis.

Caudalward displacement of the scapula (limited): by the posterior part of the Trapezius as well as of the Serratus anterior; indirectly by the Latissimus dorsi and the posterior part of the Pectoralis major.

Extension of the humerus: mainly by the Deltoideus on the whole, the Infraspinatus and the Mastohumeralis (in part), and to some extent by the Teres minor.

Flexion of the humerus: mainly by the Pectoralis major and partially by the Subscapularis.

Abduction of the humerus: mainly by the Mastohumeralis and the Supraspinatus as well as the acromial part of the Deltoideus, assisted by the anterior part of the Subscapularis, according to the position of the humerus; also by the anterior part of the Pectoralis major.

Adduction of the humerus: mainly by the Latissimus dorsi, the posterior part of the Pectoralis major, the Teres major and Teres minor, the Infraspinatus and, according to the position of the humerus, also by the posterior part of the Subscapularis.

Outward rotation: mainly by the Pectoralis major and the Infraspinatus, and, according to the position of the humerus, also by the Supraspinatus, Deltoideus and Mastohumeralis.

Inward rotation: mainly by the Latissimus dorsi and the Teres major, the posterior part of the Subscapularis, and, partially, depending on the position of the humerus, also by the Supraspinatus and the acromial part of the Deltoideus.

On the whole, the action of the highly differentiated muscles of the shoulder girdle in *Inia* brings forth rather complicated movements of the flippers in all directions. In *Tursiops, Lagenorhynchus* and other marine (pelagic) dolphins, however, the flippers are obviously moved heavily in only a few directions by more uniform muscle groups.

Discussion

It was already Jardine (1837) who mentioned that in comparison with their marine (pelagial) relatives, the river dolphins of the genera *Inia* and *Platanista* are relatively slow swimming animals. Layne (1958), who made observations on *Inia geoffrensis* in its natural habitat, was able to confirm these results. He writes: "Amazon dolphins typically swam at a leisurely pace averaging about 2 m.p.h. . . ." and describes their behavior as "generally somewhat lethargic". As to Amazon dolphins in captivity, the same behavior was observed (Layne and Caldwell 1964): "The only times they moved with greater rapidity were when they were alarmed or feeding. . . . The normal swimming speed was between 1 and 2 m.p.h. (i.e. 0.45–0.90 m/s), and the maximum speed recorded was approximately 10 m.p.h. (i.e. 4.5 m/s). . . . Free-swimming marine dolphins, however, often travel much faster, speeds from about 12 to 34 m.p.h. (i.e. 5.4–15.2 m/s) having been reported (Petersen 1925; Gray 1936; Moore 1953). Compared with these pelagial dolphins, the Amazon dolphin *Inia* appears to be an exceptionally slow swimmer."

As to the *Inia* specimens of the Zoological Garden in Duisburg, two of which were available for dissection later, Horstmannshoff (1975) calculated a swimming speed of about 1 m/s during normal activity. The authoress adds, however, that while playing or in flight, the dolphins can increase their swimming speed considerably.

In order to draw a comparison, data from Pilleri et al. (1976) about *Platanista* are added (p. 21): "When swimming slowly the swimming speed of young and subadult animals varied from 0.1–0.8 m/s. It rose to approx. 0.8–0.9 m/s during fast parallel swimming. When attacking (biting) a partner, chasing fish, in a panic situation or during pursuit by a partner it attained 1.5 m/s." Pilleri et al. (1976) continue . . ." the maximum speed of the animals recorded in a panic situation in the tank was only 1.9 m/s as against 7.8 m/s average in *Delphinus*" (p. 124).

Our own observations on live specimens of *Inia* in the Zoological Garden in Duisburg correspond with the data cited above. We have made a film about live specimens of *Inia* and *Tursiops* in order to compare their swimming behavior. *Inia* is a rather slow but extremely manoeuvrable swimmer. In accordance with Hortsmannshoff (1975) we have noticed that the *Inia* specimens were swimming nearly as often in prone as in supine position. Swimming in side position was less frequent, while one flipper, being held downward, occasionally touched the ground over longer distances, as it was reported of *Platanista* by Pilleri et al. (1976). However, in *Platanista* the side position is the most common swimming attitude: . . . "*Platanista* swims predominantly on its side in the horizontal plane . . ." (l.c.).

In *Inia*, locomotion is not only achieved by simple straightforward movements, but is completed by a whole spectrum of turns, like e.g. the rotation of the body around its long axis, the so-called "barrel-roll" movements (Layne and Caldwell 1964), or the rotation aside (yaw), and dorsalward or ventralward (pitch), these turns being correlated with a strong curvature of the body. Often the animals take an oblique or vertical position, with the head up and down, respectively. Sometimes the dolphins turn like in somersault (HERALD and DEMPSTER 1965; HORTSMANNSHOFF 1975). All these turns obviously are not conditioned only by the narrowness of the tanks in captivity but also occur in specimens of *Inia* living in their natural habitat (LAYNE 1958).

In the locomotion of *Inia,* like in all cetaceans, the trunk and the caudal fluke represent the driving element. Alterations of the direction of motion and turns are initiated by movements of the head and the highly mobile neck. The continuation and completion of manoeuvers is achieved mainly by the large and broad flippers, which also serve for the stabilisation of the equilibrium. LAYNE and CALDWELL (1964) write: "The relatively large flukes and flippers of *Inia* also appear to be correlated with its slow swimming habits, since in a slow moving dolphin larger control surfaces are probably necessary to maintain manoeuvrability and stability". Moreover, the flippers of *Inia* show an extraordinary mobility in all directions. We could observe particularly extensive inward and outward rotations (Fig. 15). In this connection both flippers are not always moved simultaneously, but are often used asyn-

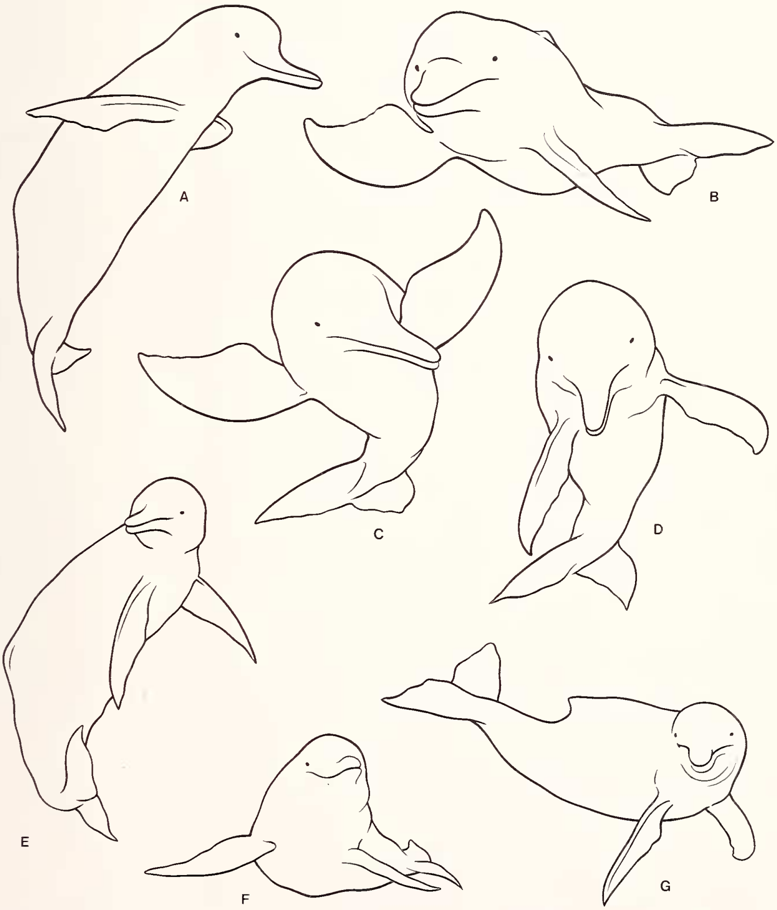

Fig. 15. Contour drawings from the frames of a film about *Inia geoffrensis* showing some phases of the movements of the flippers. Notice the extension in A and C, the flexion in D, E, and G, the abduction in B, F, and G, the adduction in A and E, the outward rotation in D, E, and G, and the inward rotation in C

chronically, as it was reported by Hortsmannshoff (1975). Layne and Caldwell write: "Another distinctive feature perhaps associated with the mode of locomotion of *Inia* is the marked flexibility of the flippers as compared to those of fast-swimming dolphins in which they mainly serve as hydroplanes. On several occasions we observed the captive *Inia*s propelling themselves very slowly forward by means of a rowing-like action of the flippers . . ."

Hence the large and rather broad flippers of *Inia* no doubt play an important role in all kinds of turning movements and can even assist in the propulsion of the body. In this respect, *Inia* not only differs from the fast-swimming marine dolphins, but also from the slow-swimming river dolphin *Platanista,* whose relatively small and narrow flippers obviously are not even involved in steering: "In these conditions it is doubtful whether the flipper in *Platanista* could have any steering capability" (Pilleri et al. 1976).

The extraordinary mobility and the biological role of the flipper in *Inia* without doubt are favored by the peculiar structure of the shoulder joint. The convergent shift of the shoulder blade and the sternum als well as the participation of the latter in the formation of the "acetabulum" for the humerus have transformed the original joint, which was widely open, into a nearly closed ball-and-socket joint, comparable to the hip joint of terrestrial mammals (Enarthrosis globoidea, Fick 1904; enarthrosis, Terry 1947). This allows a more efficient use of the muscles involved in the proper movement of the flipper, because their holding function, necessary in an "open joint", in *Inia* is largely superfluous. Moreover, the deep, complex osseous cavity of the shoulder joint can receive and easily dissipate relatively high bearing forces even in extreme positions of the flipper.

In contrast to that of the fast-swimming marine dolphins, the shoulder girdle of *Inia* shows highly differentiated muscles in correlation with a characteristic surface relief of the appropriate skeletal elements. These differences have been ascertained by comparison of *Inia* with *Tursiops, Lagenorhynchus* and *Phocoena.* Further (although indirect) confirmation for this statement was found in some works on the myology of marine dolphins as for instance Stannius (1849), Murie (1873), Sterling (1910a, b), Schulte and Smith (1918), Kunze (1912), Howell (1927, 1930), Smirnowsky (1928), Kleinenberg (1964), Sokolov and Rodionov (1974) and Purves and Pilleri (1978). On the other hand, the morphology and topography of the shoulder girdle in *Inia* in some features is rather similar to that of *Platanista,* e.g. in the powerful development of the Sterno-humero-mastoideus complex and in the occurrence of a strong Trapezius, which is largely or totally reduced in marine dolphins (Murie 1873; Howell 1930; Pilleri et al. 1976). Compared with that of *Pontoporia,* another river dolphin, the shoulder girdle of *Inia* shows nearly identical conditions (cf. Strickler 1978). For instance both species have a broad supraspinatous fossa and a well developed Supraspinatus muscle. In contrast to marine toothed whales, *Inia, Platanista* and *Pontoporia* still retain some other primitive features, e.g. the distinct Serratus anterior as well as the Omohyoideus, the latter otherwise being known of one Delphinid species only (*Delphinus*; l.c.). This tendency for the retention of manifold single muscles as well as other morphological features emphasizes the evident similarity of the fresh-water dolphins with terrestrial mammals. Analogous conditions in another muscular system of *Platanista* was recorded by Pilleri et al. (1976): "The dorsal spinal musculature is more primitive than in *Delphinus* resembling that of terrestrial mammals. In *Delphinus* the separate units become fused into a single propulsive mass".

However, the differentiation of the shoulder girdle muscles in *Inia* is much more accentuated than in *Platanista* and *Pontoporia.* This is shown in the specific tripartition of the Sterno-humero-mastoideus complex and in its connection with the Omohyoideus. Moreover, this is shown by the clear separation of the Supraspinatus and the Infraspinatus, as well as by the extraordinarily strong development of the Pectoralis major, and, finally, in the transformation of the Pectoralis minor into a coating of the accessory joint cavity of the sternum.

Thus, all of these features of *Inia* mentioned above not only have to be regarded as primitive, i.e. plesiomorphous, characters (cf. *Pontoporia*; Strickler 1978) which recall the conditions in terrestrial mammals. In addition, they stand for special adaptations of the slow-swimming *Inia* with respect to an extreme manoeuvrability in its shallow river habitat.

Table 2

Comparison of the shoulder girdle and the mode of locomotion in Inia geoffrensis and Tursiops truncatus

Inia

- flipper long and broad
- humerus long and flat, with two tubercles
- motive musculature of flipper more differentiated, insertions into humerus rather dispersed
- greater mobility of the flipper
- broad and deep articular cavity formed by both scapula and sternum
- shoulder joint represents a nearly closed ball-and socket joint (enarthrosis)
- low speeds of locomotion in shallow waters
- flippers mainly serve as manoeuvring organs (oars)

Tursiops

- flipper short and narrow
- humerus short and stout, with one common tubercle
- motive musculature of flipper less differentiated, insertions into humerus rather concentrated
- lesser mobility of the flipper
- narrow and flat articular cavity formed by the scapula only
- shoulder joint represents an unspecialized spheroidea
- high speeds of locomotion in the open sea
- flippers mainly serve as steering organs (hydroplanes)

Summary

As in most whales, the shoulder girdle in the Amazon dolphin *Inia geoffrensis* consists of two bony elements only: scapula and humerus. However, the shoulder blade has lost its original mobility, being secondarily attached to the axial skeleton by the sternum. The latter takes part in the formation of the shoulder joint, which seems to be a unique feature not only within the Cetacea, but also within the Mammalia on the whole. The anatomical peculiarities of the shoulder girdle and joint in *Inia* are characterized as follows:

1. Sternum. In contrast to the segmented sterna of most Odontoceti, the sternum in *Inia* consists of only one single bone. It is relatively large and broad, having three distinct processes on either side for the attachment of muscles and ligaments. Between these processes, the ventrolateral surface of sternum bears a shallow groove, the accessory osseous joint cavity for the humerus.
2. Scapula. In contrast to the completely plain, flattened scapulae of most whales, the shoulder blade in *Inia* shows a characteristic surface relief similar to that of terrestrial mammals. Unlike the marine dolphins, in *Inia* there is still a distinct spina scapulae separating the supraspinatous and infraspinatous fossae, the former being rather broad. In other features *Inia* again differs from the marine dolphins, e.g. in the relatively large gap between the planes of the acromion and the coracoid process (cranial view) and in the setting angle between them (lateral view) as well as in the rostroventral inclination of the coracoid process.
3. Humerus. In contrast to the very short and rounded humeri in marine dolphins, the humerus in *Inia* is relatively long and flat and shows lateral edges. There are two tubercles of humerus. Because of the special position of the flipper, the greater tubercle (being the smaller one), which serves for the insertion of the Supraspinatus only, is not situated laterally like in terrestrial mammals but cranioventrally. For the same reason the lesser tubercle (being the larger one), which serves for the insertion of the strong Subscapularis, is situated medioventrally. Apart from this, the arrangement of the head of

humerus and both tubercula in *Inia* principally corresponds to the conditions in man. In *Tursiops* and other marine dolphins, however, there is only one (secondary) common tubercle which (like the head of humerus) seems to have been "rotated" by approx. 90° outward around the long axis of the flipper and thus arises from the dorsolateral surface of humerus.

4. Structure of the shoulder joint. In *Inia* the hemispherical head of the humerus is fitted into the cup-shaped "acetabulum" which is composed of the glenoid cavity of the scapula, situated dorsally, and the accessory joint cavity of the sternum, situated medioventrally. The humeral and scapular parts of the joint are covered with a layer of hyaline cartilage, the sternal part is covered with a thick layer of collagen and elastic fibers derived from the aponeurosis of the Pectoralis minor. A wide and folded articular capsule encloses the roomy synovial cavity, being strengthened by some ligaments. Three of them attach the sternum to both of the other components of the shoulder joint: the sternoacromial, sternoglenoidal, and sternohumeral ligaments.
5. Musculature. In accordance with the characteristics of the skeletal elements mentioned above, the flipper muscles in *Inia* are highly differentiated and show many separate, rather dispersed insertions into the humerus. In *Tursiops* and other marine dolphins, however, the flipper muscles tend to be inserted into the (secondary) common tubercle of humerus. A separate (additional) head of the Sterno-humero-mastoideus complex, which is fused with the Omohyoideus, has been found characteristic for *Inia* as well as the partial differentation of the Pectoralis minor into a coating of the sternal part of the "acetabular" cavity.
6. Muscle action. In *Tursiops* and other marine dolphins, the muscles of the shoulder girdle seem to be specialized in powerful movements of the flippers in a few directions only, mainly in extension/abduction and less in flexion/adduction. In *Inia*, however, the accent lies on variable and extensive, less powerful movements of the flippers in all directions, including inward and outward rotation.
7. The functional significance of the shoulder joint. The relatively large flippers of *Inia* can be rotated extensively in all directions by the highly differentiated appropriate musculature. Like oars, they actively take part in all kinds of turns and even in the propulsion of the body. Because of the unique articulation of the humerus with both scapula and sternum (enarthrosis), the flippers of *Inia* can work effectively even in extreme positions. By this *Inia geoffrensis* attains a particularly high manoeuvrability which should be an advantage in the shallow waters of the Amazon river system.

Zusammenfassung

Morphologie des Schultergürtels beim Amazonas-Delphin Inia geoffrensis mit besonderer Berücksichtigung des Schultergelenks und der Bewegungen der Flipper

Wie bei den meisten Vertretern der Cetacea besteht der Schultergürtel des Amazonas-Delphins *Inia geoffrensis* nur aus zwei Elementen, Scapula und Humerus. Jedoch hat hier das Schulterblatt seine ursprüngliche Beweglichkeit eingebüßt, indem es über das Sternum (sekundär) am Achsenskelett aufgehängt ist. Darüber hinaus beteiligt sich das Sternum an der Bildung des Schultergelenks, was nicht nur innerhalb der Cetacea, sondern auch der Mammalia insgesamt einen Sonderfall darstellt. Die anatomischen Besonderheiten des Schultergürtels und des Schultergelenks sind folgendermaßen charakterisiert:

1. Sternum. Im Gegensatz zu den segmentierten Sterna der meisten Odontoceti liegt jenes von *Inia* als einheitliches Element vor. Es ist verhältnismäßig lang, ziemlich breit und weist jederseits drei deutliche Fortsätze auf, welche der Anheftung von Muskeln und Ligamenten dienen. Zwischen diesen Fortsätzen befindet sich auf der lateroventralen Fläche des Sternums eine flache Grube, die akzessorische Gelenkpfanne für den Humerus.
2. Scapula. Anders als bei den meisten Walen, bei denen sie völlig eben ist, weist die Scapula von *Inia* ein charakteristisches Oberflächenrelief auf und erinnert damit an die Situation bei den landlebenden Säugetieren. Im Gegensatz zu den marinen Delphinen ist bei *Inia* noch eine deutliche Spina scapulae vorhanden, welche die Fossae supraspinata und infraspinata voneinander trennt, wobei die erstere hier noch ziemlich breit ist. Auch in anderen Merkmalen weicht *Inia* von den marinen Delphinen ab, so in der verhältnismäßig breiten Lücke zwischen den Ebenen von Acromion und Processus coracoideus (Cranialansicht) und in dem Anstellwinkel zwischen beiden Fortsätzen (Lateralansicht), sowie in der Neigung des Processus coracoideus rostroventrad.
3. Humerus. Während die marinen Delphine sehr kurze und verrundete Humeri aufweisen, ist jener von *Inia* verhältnismäßig lang, flach und mit seitlichen Kanten versehen. Zwei Tubercula sind vorhanden. Infolge der speziellen Haltung des Flippers ist das (kleinere) Tuberculum majus, welches lediglich dem M. supraspinatus als Insertionsfläche dient, nicht lateral gelegen wie bei Landsäugetieren, sondern cranioventral. Das (größere) Tuberculum minus, welches der Insertion des kräftigen M. subscapularis dient, ist aus demselben Grund medioventral gelegen. Im übrigen entspricht die räumliche Zuordnung des Humeruskopfes und der beiden Tubercula zueinander bei *Inia* prinzipiell der Situation beim Menschen. Bei *Tursiops* und anderen marinen Delphinen ist dagegen nur ein (sekundäres) gemeinsames Tuberculum vorhanden, welches (wie auch der Humeruskopf) ungefähr 90° um die Längsachse des Flippers „außenrotiert" scheint und infolgedessen von der dorsolateralen Fläche des Humerusschaftes aufragt.

4. Bau des Schultergelenks. Bei *Inia* ist der halbkugelförmige Humeruskopf in das stark eingetiefte ,,Acetabulum" eingepaßt, welches aus der dorsal gelegenen Gelenkpfanne der Scapula und der medioventral gelegenen akzessorischen Gelenkgrube des Sternums besteht. Die Gelenkflächen von Humerus und Scapula sind mit einer Schicht hyalinen Knorpels überzogen, jene des Sternums mit einer dicken Schicht aus kollagenen und elastischen Fasern, welche sich aus der Aponeurose des M. pectoralis minor ableitet. Die weite und gefaltete Gelenkkapsel umschließt eine geräumige Gelenkhöhle und ist durch einige Ligamente verstärkt. Drei davon befestigen das Sternum an den beiden übrigen Komponenten des Schultergelenks, die Ligg. sternoacromiale, sternoglenoidale und sternohumerale.
5. Muskulatur. Im Einklang mit den obengenannten Charakteristika der Skelettelemente sind die Flippermuskeln von *Inia* stark differenziert und weisen einzelne, ziemlich zerstreute Insertionen am Humerus auf. Bei *Tursiops* und anderen marinen Delphinen hingegen neigen die Flippermuskeln dazu, an einem (sekundär entstandenen) gemeinsamen Tuberculum des Humerus zu inserieren. Das Auftreten eines zusätzlichen Kopfes im Sterno-humero-mastoideus-Komplex und seine Fusion mit dem M. omohyoideus sind für *Inia* charakteristisch, desgleichen die partielle Differenzierung des M. pectoralis minor zu einer Auskleidung des sternalen Teils des ,,Acetabulums".
6. Muskelfunktion. Bei *Tursiops* und anderen marinen Delphinen scheint die Schultergürtelmuskulatur auf kräftige Bewegungen der Flipper in nur wenigen Richtungen spezialisiert, vor allem auf Extension/Abduktion, weniger auf Flexion/Adduktion. Dagegen liegt bei *Inia* der Akzent auf mannigfaltigen und umfangreichen, weniger kräftigen Bewegungen der Flipper in sämtlichen Richtungen des Raumes, Außen- und Innenrotation inbegriffen.
7. Die funktionelle Bedeutung des Schultergelenks. Die verhältnismäßig großen Flipper von *Inia* können durch die zugehörige, hochdifferenzierte Muskulatur extensiv in allen Richtungen des Raumes gedreht werden. Sie nehmen wie Ruder aktiv an jeder Art von Drehung und sogar an der Propulsion des Körpers teil. Infolge der einzigartigen Gelenkung des Humerus sowohl mit der Scapula als auch mit dem Sternum (Nußgelenk) können die Flipper von *Inia* auch in extremen Stellungen effektiv arbeiten. *Inia geoffrensis* erhält dadurch eine besonders hohe Manövrierfähigkeit, welche in den flachen Gewässern des Amazonas-Systems von Vorteil sein dürfte.

Acknowledgements

We are most grateful to Dr. P. J. H. van Bree, Amsterdam, for the suggestion of the present investigation and for the generous supply with material of the Cetacea. Dr. W. Gewalt is thanked for his kind help with material of *Inia geoffrensis* and the permission to take films in the Zoological Garden in Duisburg, Dr. D. Kock of the Forschungsinstitut Senckenberg in Frankfurt a. M. for making available a skeleton of *Inia geoffrensis*, and Mr. G. Behrmann, Bremerhaven, for valuable informations concerning the presence of the clavicle in *Pseudorca*. We are also much obliged to several members of the Dr. Senckenbergische Anatomie, Mr. S. Eckardt for the kind loan of material, Mr. H. L. Schneeberger for making the drawings, Mr. J. Herforth for the preparation of photos, and Mrs. U. Bremer and Ms. I. Giesendorf for technical assistance. Dr. W. K. Schwerdtfeger of the Max-Planck-Institut für Hirnforschung (Frankfurt am Main) is thanked for kindly reading the English manuscript.

Abbreviations

abd	Abduction
,,acet"	,,Acetabulum" (glenoid cavity of scapula + accessory joint cavity of sternum)
acr	Acromion
acr. marg. ligg	Acromiomarginal ligaments
add	Adduction
art. caps	Articular capsule of the shoulder joint
c	Center of head of humerus (in cranial view)
coll	Collagen fibers
comm. tub	Common tubercle of humerus
cor. acr. lig	Coracoacromial ligament
cor. marg. ligg	Coracomarginal ligaments
later. surf	Lateral surface of scapula
latiss	Latissimus dorsi muscle
levat. scap	Levator scapulae muscle
manub	Manubrium of sternum
marg. med	Margo vertebralis of scapula
marg. sup	Margo superior of scapula
mast. hum	Mastohumeralis muscle
omohyo	Omohyoideus muscle
out	Outward rotation
pec. maj	Pectoralis major muscle
pec. min	Pectoralis minor muscle
r 1,2,3	Ribs 1,2,3
radial b	Radial border of humerus
scap	Scapula
serrat	Serratus anterior muscle
spin	Spine of scapula
ster	Sternum